Cats increase fatty acid oxidation when isocalorically fed meat-based diets with increasing fat content

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Lester, Tammy, Gail Czarnecki-Maulden, and Douglas Lewis. Cats increase fatty acid oxidation when isocalorically fed meat-based diets with increasing fat content. Am. J. Physiol. 277 (Regulatory Integrative Comp. Physiol. 46): R878–R886, 1999.—This study tested the hypothesis that sedentary cats have the ability to adapt to high-fat carnivore diets by increasing fat oxidation. Twenty-four hour indirect calorimetry was used to determine total energy expenditure (TEE) and macronutrient oxidation in six vasectomized male (VAS) and six ovariectomized female (OVX) cats isocalorically fed lower-fat (53% fat, 45% protein) and higher-fat (71% fat, 26% protein) meat-based diets at maintenance for 8 days. Fat oxidation increased linearly with fat intake with a mean slope of 0.91 g fat oxidized/g fat intake (P < 0.001), with no change in TEE. However, VAS male cats were able to more precisely match fat oxidation with fat intake than OVX female cats (P < 0.02). Body fat content did not significantly influence fat oxidation. These results demonstrate that cats maintain body weight during short-term isocaloric feeding of a high-fat carnivore-type diet in part by increasing fat oxidation concomitantly with increases in fat intake. This ability may be an important mechanism underlying the resistance of cats to obesity, despite habitual consumption of high-fat diets.

respiratory quotient; high-fat diets; carnivore; obesity; macronutrient utilization

IT IS WELL ESTABLISHED that overfeeding high-fat diets promotes obesity in humans and rodents (5, 13, 19, 33, 35). There are several mechanisms by which high-fat diets induce weight gain. First, high-fat diets increase energy intake because of decreased satiation (12) and hyperphagia (27, 43). Second, high-fat diets also increase energy storage because fat is energy dense and is stored more efficiently than the other macronutrients (14, 38). Third, high-fat diets do not promote fat oxidation (15).

However, it is not clear whether consumption of high-fat diets at or near an animal’s maintenance energy requirement (MER) results in the accumulation of fat and subsequent weight gain. In humans, isocaloric feeding of 0 to 70% fat as energy did not affect the energy requirement for weight maintenance (26). A cross-sectional study also indicated that dietary fat plays only a minor role in overall adiposity (23). Conversely, self-reported energy and fat intakes of obese and lean individuals suggest that fat intake, independent of energy intake, plays an important role in fat deposition (31, 35). Similarly, Sheppard et al. (41) reported that weight loss was more strongly associated with the decrease in fat energy than with a change in total energy intake. In contrast to humans, long-term feeding studies with rats demonstrate that high-fat diets consistently increase body weight and fat mass to a greater extent than high-carbohydrate diets under isocaloric feeding conditions (19, 33, 40, 46).

The conflicting studies concerning the role of high-fat diets fed at maintenance energy intakes on body weight and fat deposition in humans may be due to heterogeneity of the individuals studied. Consumption of a high-fat diet increased fat storage in postobese women but not in lean women (5). Similarly, Chang et al. (9) reported that obesity-resistant rats had a greater relative rate of fat oxidation than obesity-prone rats when fed 60% fat diets, although no difference in energy expenditure was found between groups.

Cats (*Felis domesticus*) normally consume a very high-fat diet (>50% of kcal), yet the reported incidence of feline overweight and obesity ranges from 6 to 12% in the 1970s (3) to 25% in the 1990s (39). Only 4.5% of over 2,000 United States domestic cats were judged to be obese (39). Although few studies have addressed the pathogenesis of feline obesity, inactivity, gonadectomy, and the consumption of dry food have been implicated as risk factors (11, 16, 37, 39, 42). One way most cats are able to maintain body weight on high-fat diets is their apparent lack of hyperphagia when fed high-fat and/or energy-dense diets (8, 20). In the present study, the metabolic response of sedentary cats to high-fat meat-based diets was determined. The hypothesis tested was that cats, challenged with a high-fat meat-based diet, adapt by increasing fat oxidation when fed at MER.

MATERIALS AND METHODS

Animals. Six vasectomized male (VAS) and six ovariectomized (at least 4 yr before this study) female (OVX) domestic short-hair cats were selected from ~64 cats previously enrolled in a 6-mo feeding trial involving ad libitum feeding of five different diets with similar nutrient composition. The nutrient composition of the trial diets was similar to the basal diet used in this experiment. Over 90% of these cats maintained body weight within 5% Cats whose weight varied by 10.2±0.32±0.247 on July 5, 2017 http://ajpregu.physiology.org/ Downloaded from by 10.22032.247 on July 5, 2017
iments. Cats were petted and held several times daily during feeding, cage cleaning, weighing, and urine or feces collection. The animal care committee of Friskies Research and Development (St. Joseph, MO) and Iowa State University approved the experimental protocol.

Diet composition. The macronutrient compositions of the three canned diets fed during the study are reported in Table 1. The lower- and higher-fat meat-based diets were wholly manufactured from chicken parts, with vitamin and mineral supplements, and represent extremes in fat content for a canned diet that will maintain acceptable consistency and palatability for cats. The amino acid and fatty acid compositions of the lower- and higher-fat diets are reported in Tables 2 and 3, respectively. Each diet was fed for 8 days, 7 days before, and including the 24-h indirect calorimetry period on day 8. To measure the metabolic response of cats to increasing dietary fat with a constant energy intake, the diets were fed in the following order after an initial 30-day baseline period: lower fat (53% energy as fat), baseline (62% as fat), and higher fat (71% as fat).

Determination of MER. To normalize the cats to a single diet, we fed Friskies Beef and Liver as the baseline diet due to its similarity in macronutrient composition to the diets fed during the preceding 6-mo feeding trial. MER was determined after a 1-mo ad libitum feeding of the baseline diet and was based on mean daily intake over 5 days. The lower- and higher-fat meat-based diets were fed isocalorically at each animals’ MER. Daily caloric intake was calculated based on macronutrient composition using physiological fuel values of 3.5, 8.5, and 3.5 kcal/g for protein, fat, and carbohydrate, respectively (1).

Determination of body composition. Body composition was determined during the 30-day normalization period using dual-energy X-ray absorptiometry. Approximately 10 min before anesthesia induction, all cats were given atropine sulfate (0.4 mg/kg) intramuscularly. Cats were then anesthetized by intravenous injection of 10 mg/kg ketamine hydrochloride and 0.5 mg/kg diazepam, and the anesthesia was maintained with isoflurane gas administered via an endotracheal tube. A licensed veterinary technician continually monitored the cats. Total body scans were performed on a Lunar DPX-alpha scanner (Lunar, Madison, WI) operating in small pediatric mode. Cats were placed on the table in the prone position, with legs placed adjacent to the body and paws pointing caudally. Quality assurance scans were performed each day using a Lunar standard before commencing animal scans. All of the cats were judged to be nonobese by a licensed veterinarian based on body condition scoring. Body weight of each cat was within two SDs from the mean weight for the mature cat population, and the body fat of each cat was <30% of body weight.

Urine and fecal collection. The metabolic cages in which the animals were housed consisted of a raised wire floor overlying a sloped bottom that emptied into a stainless steel cup. A quantitative, 3-day collection of urine and feces was made for all animals beginning on day 5 of each diet. Iron sulfate (1 g/kg) was added to the diet as a fecal marker on day 5 and again 72 h later. Fecal collection began on the first day the marker appeared in the feces and continued until, but did not include, the day the marker reappeared. Fecal samples were collected daily from the metabolic cage and as necessary from the calorimeter chamber. Pooled fecal samples were stored initially at −14°C, then desiccated, ground, weighed, and stored at room temperature until analysis for gross energy by adiabatic bomb calorimetry. Urine was collected daily for 72 h immediately preceding calorimetry. Urine was collected with 10 ml of sulfuric acid added as a preservative and was stored at −14°C until nitrogen analysis. The 24-h urine output was estimated by dividing the 72-h pooled samples by three.

Table 1. Nutrient composition of the experimental diets

<table>
<thead>
<tr>
<th>Component</th>
<th>Baseline</th>
<th>Lower Fat</th>
<th>Higher Fat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percent by Weight</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water</td>
<td>76.8</td>
<td>78.2</td>
<td>76.7</td>
</tr>
<tr>
<td>Protein</td>
<td>11.0</td>
<td>13.3</td>
<td>9.8</td>
</tr>
<tr>
<td>Fat</td>
<td>8.6</td>
<td>6.6</td>
<td>10.9</td>
</tr>
<tr>
<td>Ash</td>
<td>1.9</td>
<td>1.3</td>
<td>1.4</td>
</tr>
<tr>
<td>Carbohydrate</td>
<td>1.7</td>
<td>0.6</td>
<td>1.2</td>
</tr>
<tr>
<td>ME, kcal/g</td>
<td>1.2</td>
<td>1.0</td>
<td>1.3</td>
</tr>
<tr>
<td>Percent Total Energy</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fat</td>
<td>62.2</td>
<td>53.5</td>
<td>70.7</td>
</tr>
<tr>
<td>Protein</td>
<td>32.7</td>
<td>44.6</td>
<td>26.2</td>
</tr>
<tr>
<td>Carbohydrate</td>
<td>5.1</td>
<td>1.9</td>
<td>3.1</td>
</tr>
</tbody>
</table>

Nutrient composition was determined by proximate analysis at Friskies Research and Development. ME, metabolizable energy.

Table 2. Amino acid composition of lower- and higher-fat diets

<table>
<thead>
<tr>
<th>Amino Acid</th>
<th>Lower-Fat Diet</th>
<th>Higher-Fat Diet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aspartate</td>
<td>1.06</td>
<td>0.78</td>
</tr>
<tr>
<td>Threonine</td>
<td>0.58</td>
<td>0.44</td>
</tr>
<tr>
<td>Serine</td>
<td>0.52</td>
<td>0.41</td>
</tr>
<tr>
<td>Glutamate</td>
<td>1.79</td>
<td>1.25</td>
</tr>
<tr>
<td>Proline</td>
<td>0.59</td>
<td>0.52</td>
</tr>
<tr>
<td>Glycine</td>
<td>0.76</td>
<td>0.68</td>
</tr>
<tr>
<td>Alanine</td>
<td>0.81</td>
<td>0.60</td>
</tr>
<tr>
<td>Cysteine</td>
<td>0.09</td>
<td>0.07</td>
</tr>
<tr>
<td>Valine</td>
<td>0.66</td>
<td>0.50</td>
</tr>
<tr>
<td>Methionine</td>
<td>0.33</td>
<td>0.22</td>
</tr>
<tr>
<td>Isoleucine</td>
<td>0.59</td>
<td>0.40</td>
</tr>
<tr>
<td>Leucine</td>
<td>1.03</td>
<td>0.77</td>
</tr>
<tr>
<td>Tyrosine</td>
<td>0.45</td>
<td>0.34</td>
</tr>
<tr>
<td>Phenylylalanine</td>
<td>0.54</td>
<td>0.41</td>
</tr>
<tr>
<td>Lysine</td>
<td>1.06</td>
<td>0.73</td>
</tr>
<tr>
<td>Histidine</td>
<td>0.43</td>
<td>0.25</td>
</tr>
<tr>
<td>Arginine</td>
<td>0.85</td>
<td>0.63</td>
</tr>
</tbody>
</table>

Values represent % by weight. Determined by Friskies Research and Development analytical laboratory.

Table 3. Fatty acid composition of the lower- and higher-fat diets

<table>
<thead>
<tr>
<th>Fatty Acid</th>
<th>Lower-Fat Diet</th>
<th>Higher-Fat Diet</th>
</tr>
</thead>
<tbody>
<tr>
<td>14:0 Myristic acid</td>
<td>0.61*</td>
<td>0.64</td>
</tr>
<tr>
<td>14:1 Myristolic acid</td>
<td>0.20</td>
<td>0.21</td>
</tr>
<tr>
<td>15:0 Pentadecanoic acid</td>
<td>0.08</td>
<td>0.08</td>
</tr>
<tr>
<td>16:0 Palmitic acid</td>
<td>23.61</td>
<td>23.59</td>
</tr>
<tr>
<td>16:1 Palmitoleic acid</td>
<td>6.99</td>
<td>7.07</td>
</tr>
<tr>
<td>17:0 Margaric acid</td>
<td>0.12</td>
<td>0.13</td>
</tr>
<tr>
<td>17:1 Margaroleic acid</td>
<td>0.09</td>
<td>0.09</td>
</tr>
<tr>
<td>18:0 Stearic acid</td>
<td>6.83</td>
<td>6.72</td>
</tr>
<tr>
<td>18:1 Oleic acid</td>
<td>38.45</td>
<td>39.04</td>
</tr>
<tr>
<td>18:1 Elaidic acid</td>
<td>2.20</td>
<td>2.19</td>
</tr>
<tr>
<td>18:2 Linoleic acid</td>
<td>15.49</td>
<td>15.16</td>
</tr>
<tr>
<td>18:3 γ-Linolenic acid</td>
<td>0.23</td>
<td>0.22</td>
</tr>
<tr>
<td>18:3 Linolenic acid</td>
<td>0.63</td>
<td>0.67</td>
</tr>
<tr>
<td>20:0 Arachidonic acid</td>
<td>0.12</td>
<td>0.08</td>
</tr>
<tr>
<td>20:1 Eicosanonic acid</td>
<td>0.32</td>
<td>0.28</td>
</tr>
<tr>
<td>20:4 Arachidonic acid</td>
<td>1.37</td>
<td>1.19</td>
</tr>
</tbody>
</table>

Values represent % of total. Determined by Friskies Research and Development analytical laboratory.
Nitrogen excretion was determined using a Kjeltech autoanalyzer (Tecator, Herndon, VA).

Digestible energy. Digestible energy is defined as the total energy intake less the energy in the feces. The digestible energy of each diet (baseline, low fat, and high fat) was determined by measuring the total energy intake of each animal corresponding to the 3-day fecal collection and subtracting the 3-day total gross energy of the feces.

Indirect calorimetry. O₂ intake (V˙O₂) and CO₂ production (V˙CO₂) were measured using an open-circuit Oxymax system (Columbus Instruments, Columbus, OH) consisting of two positive-pressure Plexiglas chambers (50 × 50 × 60 cm, 125 liters). The air inside the chamber is mixed with the help of a fan. A paramagnetic O₂ analyzer measured O₂ concentration, and CO₂ concentration was measured by infrared spectrophotometry. Temperature was maintained at 25 ± 1°C. Air samples were drawn from each chamber every 5 min for determination of V˙O₂ and V˙CO₂. Animals were habituated to the chambers over 1 wk for periods of 2, 4, and 6 h. Animals were considered to have habituated adequately when they exhibited normal behavior, i.e., movement, eating, and drinking. Calibration of the calorimeter was performed daily using standard gas mixtures (20.5% O₂ and 0.5% CO₂). The nonprotein respiratory quotient (NPRQ) and substrate oxidation were calculated based on the following formulas (28).

\[ \text{NPRQ} = \frac{[V\dot{O}_2 - (\text{urinary N} \times 6.25 \times 0.966)]}{[V\dot{O}_2 - (\text{urinary N} \times 6.25 \times 0.996)]} \]

where 6.25 is the conversion for nitrogen to protein, 0.975 is the number of liters of CO₂ produced per gram of protein oxidized, and 0.966 the number of liters of O₂ consumed per gram of protein oxidized. The caloric equivalent per liter of nonprotein O₂ and proportions of carbohydrate and fat oxidized were determined based on the NPRQ tables as given by Lusk (28).

Statistical analyses. Statistical analyses were carried out using Systat (Systat, Evanston, IL). Data were analyzed by ANOVA with repeated measures with sex status (VAS male; OVX, ovariectomized female) as the trial factor. Body fat was also added as an independent variable to the general model that was used to analyze the effects of sex status, body fat (leaner, fatter) and diet (trial factor), and their interactions on the dependent variables. Associations of MER and body composition with dependent variables were analyzed using univariate linear regression. The significance level was set at α = 0.05, but we also report differences with α < 0.10 to better balance the type I and type II statistical errors. Total intakes (days 1–7 plus day 8 in calorimeter), day 7 intake (day preceding calorimetry), and the intake for the day in the calorimeter chamber (day 8) were analyzed. Days 7 and 8 energy and macronutrient intakes were not significantly different from the total intakes measured over the entire 8-day experimental diet period. Only the 8-day intakes are reported.

RESULTS

The sex status, age, weight, body composition, and MER of the cats studied are reported in Table 4. VAS male cats weighed significantly more than OVX female cats (4.5 ± 0.8 vs. 4.1 ± 0.7 kg, P < 0.03, means ± SD) due to greater lean mass (3.6 ± 0.6 vs. 3.0 ± 0.5 kg, P < 0.02). Sex status did not affect MER or percent body fat. However, four of six OVX female cats had body fat values exceeding 14% of weight, compared with only two of six VAS male cats.

Energy intake, macronutrient intake, and weight maintenance. Average daily energy intake (kcal) was positively correlated with body weight \(^{0.68}\) on both the lower- and higher-fat diets (r = 0.72 and 0.85, P < 0.05; Fig. 1, A and B, respectively). There was no significant difference in average daily energy intake on the lower- or higher-fat diets (874 ± 255 vs. 907 ± 255 kJ). Digestible energy was similar on both the lower- and higher-fat meat-based diets (89 ± 3% lower fat vs. 89 ± 3% higher fat). The macronutrient intakes of VAS male and OVX female cats fed the lower- and higher-fat diets are summarized in Table 5. By design, cats fed the higher-fat diet consumed significantly more fat (P = 0.001) and significantly less protein (P = 0.001). VAS male cats tended to consume more total energy, fat, protein, and carbohydrate compared with OVX female cats (P < 0.1). When expressed per kilogram body weight, the differences in total caloric intake were most pronounced on the lower-fat diet, with VAS male cats consuming 49% more calories than OVX female cats. The higher-fat diet was associated with 36% greater total caloric intake for VAS male cats compared with OVX female cats.

Table 4. Characteristics of cats

<table>
<thead>
<tr>
<th>ID</th>
<th>Age, yr</th>
<th>Initial Wt, kg</th>
<th>Body Fat, %</th>
<th>Lean Mass, kg</th>
<th>MER, kcal/kg</th>
</tr>
</thead>
<tbody>
<tr>
<td>VAS Males</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B148</td>
<td>12</td>
<td>4.855</td>
<td>15.9</td>
<td>4.083</td>
<td>60.9</td>
</tr>
<tr>
<td>G437</td>
<td>9</td>
<td>5.038</td>
<td>22.8</td>
<td>3.889</td>
<td>57.6</td>
</tr>
<tr>
<td>G468</td>
<td>9</td>
<td>4.930</td>
<td>8.0</td>
<td>4.536</td>
<td>55.7</td>
</tr>
<tr>
<td>B180</td>
<td>10</td>
<td>5.338</td>
<td>5.2</td>
<td>5.060</td>
<td>70.0</td>
</tr>
<tr>
<td>G388</td>
<td>10</td>
<td>3.422</td>
<td>4.9</td>
<td>3.254</td>
<td>68.4</td>
</tr>
<tr>
<td>G855</td>
<td>4</td>
<td>3.637</td>
<td>4.3</td>
<td>3.481</td>
<td>66.2</td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>9 ± 3</td>
<td>4.537 ± 0.800</td>
<td>10.2 ± 7.5</td>
<td>4.051 ± 0.669</td>
<td>63.1 ± 5.9</td>
</tr>
<tr>
<td>OVX Females</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A147</td>
<td>14</td>
<td>4.143</td>
<td>28.3</td>
<td>2.971</td>
<td>42.0</td>
</tr>
<tr>
<td>A172</td>
<td>12</td>
<td>3.117</td>
<td>25.9</td>
<td>2.310</td>
<td>56.1</td>
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<tr>
<td>G372</td>
<td>10</td>
<td>4.490</td>
<td>14.4</td>
<td>3.843</td>
<td>51.5</td>
</tr>
<tr>
<td>A151</td>
<td>14</td>
<td>3.300</td>
<td>7.3</td>
<td>3.059</td>
<td>54.9</td>
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<td>G411</td>
<td>10</td>
<td>3.843</td>
<td>17.2</td>
<td>3.182</td>
<td>76.2</td>
</tr>
<tr>
<td>G746</td>
<td>5</td>
<td>2.852</td>
<td>4.7</td>
<td>2.718</td>
<td>87.7</td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>11 ± 3</td>
<td>3.624 ± 0.636</td>
<td>16.3 ± 9.6</td>
<td>3.014 ± 0.510</td>
<td>61.4 ± 17.1</td>
</tr>
</tbody>
</table>

Body fat was determined by dual energy X-ray absorptiometry. ID, identification no.; MER, maintenance energy requirement; VAS, vasectomized male; OVX, ovariectomized female.
weight, energy and macronutrient intake were not affected by sex status (data not presented). All cats maintained their initial weight within an average of ±2% throughout the experiment (Fig. 2).

Diet effects on energy expenditure and macronutrient oxidation. Total 24-h energy expenditure (TEE) was positively correlated with body weight 0.66 on both the lower- and higher-fat diets ($r = 0.69$ and $0.82$, $P < 0.05$; Fig. 1, C and D, respectively). Similar results were obtained when data were expressed per kilogram lean body mass (data not presented). Increasing the dietary fat content from 53 to 71% of energy increased total fat oxidation by 64% ($P < 0.001$), decreased total carbohydrate oxidation by 44% ($P < 0.03$), but did not affect total protein oxidation (Table 5). The net change in macronutrient intake and oxidation that occurred when cats were switched from the lower-fat to the higher-fat diet is reported in Fig. 3. Increased fat intake from the higher-fat diet was precisely matched by an increase in fat oxidation, whereas protein and carbohydrate intakes from the higher-fat diets were not matched by oxidation. In all cats, fat oxidation increased linearly with dietary fat intake with a mean slope of 0.91 (Fig. 4).

Sex status effects on energy expenditure and macronutrient oxidation. Similar to energy intake, VAS male cats tended to expend more total energy compared with OVX female cats (Table 5, $P < 0.07$), but the difference between VAS and OVX cats was not significant when TEE was expressed per kilogram body weight (data not shown).

Feeding diets with increasing dietary fat as percent of energy increased fat oxidation to a greater extent in VAS male compared with the OVX female cats ($P < 0.001$). Fat oxidation on the lower-fat diet was not significantly influenced by sex status. Similar results were obtained when fat oxidation was expressed per kilogram body weight (data not presented). Sex status did not significantly affect carbohydrate or protein oxidation (Table 5).

Effect of body fat on macronutrient oxidation. Cats were grouped according to body fat into leaner (<14% body fat, $5.7 \pm 1.6\%$, mean ± SD, $n = 6$) and fatter
Table 5. Energy and macronutrient intake and expenditure and NPRQ in VAS and OVX cats fed low- and high-fat meat-based diets

<table>
<thead>
<tr>
<th>Variable</th>
<th>Sex Status</th>
<th>Low Fat (53%)</th>
<th>High Fat (71%)</th>
<th>Effects</th>
</tr>
</thead>
<tbody>
<tr>
<td>Energy, kJ</td>
<td>VAS</td>
<td>958 ± 311</td>
<td>1,044 ± 287</td>
<td>0.06 0.09 0.09</td>
</tr>
<tr>
<td></td>
<td>OVX</td>
<td>772 ± 148</td>
<td>774 ± 138</td>
<td></td>
</tr>
<tr>
<td>Fat, g</td>
<td>VAS</td>
<td>14.7 ± 4.7</td>
<td>20.7 ± 5.7</td>
<td>0.001 0.09 0.020</td>
</tr>
<tr>
<td></td>
<td>OVX</td>
<td>11.6 ± 2.2</td>
<td>15.4 ± 2.7</td>
<td></td>
</tr>
<tr>
<td>Protein, g</td>
<td>VAS</td>
<td>29.7 ± 9.5</td>
<td>18.7 ± 5.1</td>
<td>0.001 0.10 NS</td>
</tr>
<tr>
<td></td>
<td>OVX</td>
<td>23.5 ± 4.5</td>
<td>13.9 ± 2.5</td>
<td></td>
</tr>
<tr>
<td>Carbohydrate, g</td>
<td>VAS</td>
<td>1.2 ± 0.4</td>
<td>2.2 ± 0.6</td>
<td>0.001 0.09 0.025</td>
</tr>
<tr>
<td></td>
<td>OVX</td>
<td>1.1 ± 0.1</td>
<td>1.7 ± 0.3</td>
<td></td>
</tr>
<tr>
<td>NPRQ</td>
<td>VAS</td>
<td>0.82 ± 0.02</td>
<td>0.75 ± 0.01</td>
<td>0.001 0.03 NS</td>
</tr>
<tr>
<td></td>
<td>OVX</td>
<td>0.84 ± 0.02</td>
<td>0.79 ± 0.02</td>
<td></td>
</tr>
<tr>
<td>Total 8-Day Intakes</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Energy, kJ</td>
<td>VAS</td>
<td>730 ± 143</td>
<td>885 ± 121</td>
<td>NS 0.07 NS</td>
</tr>
<tr>
<td></td>
<td>OVX</td>
<td>730 ± 98</td>
<td>703 ± 85</td>
<td></td>
</tr>
<tr>
<td>Fat, g</td>
<td>VAS</td>
<td>7.0 ± 1.8</td>
<td>13.3 ± 1.3</td>
<td>0.001 0.09 0.001</td>
</tr>
<tr>
<td></td>
<td>OVX</td>
<td>6.9 ± 2.2</td>
<td>9.6 ± 1.6</td>
<td></td>
</tr>
<tr>
<td>Protein, g</td>
<td>VAS</td>
<td>19.6 ± 11.6</td>
<td>16.6 ± 6.5</td>
<td>NS 0.09 NS</td>
</tr>
<tr>
<td></td>
<td>OVX</td>
<td>14.1 ± 3.7</td>
<td>11.0 ± 3.6</td>
<td></td>
</tr>
<tr>
<td>Carbohydrate, g</td>
<td>VAS</td>
<td>13.2 ± 7.2</td>
<td>6.5 ± 2.2</td>
<td>0.023 NS NS</td>
</tr>
<tr>
<td></td>
<td>OVX</td>
<td>14.0 ± 3.4</td>
<td>9.4 ± 2.0</td>
<td></td>
</tr>
</tbody>
</table>

Data for low- and high-fat diets are means ± SD. Data for effects are P values. NPRQ, nonprotein respiratory quotient. NS, not significant.

Fig. 2. Weight maintenance of adult cats (n = 12) on 3 meat-based diets. Data points are group means. There was no significant change in weight over time (P > 0.05).

Fig. 3. Change in macronutrient intake and oxidation in cats fed the lower-fat and then the higher-fat diets. Change in macronutrient was calculated by subtracting the intake and oxidation rates (g) on the lower-fat diet from the macronutrient intake and oxidation rates on the higher-fat diet. (>14% body fat, 20.5 ± 5.4%, n = 6) groups. The fatter cats weighed slightly more than the leaner cats, but the difference was not significant (P > 0.10). Overall, there was no significant difference between leaner (5.7 ± 1.6% body fat, n = 6) and fatter (20.5 ± 5.4% body fat, n = 6) cats in matching fat oxidation with the increase in fat intake as cats went from the lower-fat diet to the higher-fat diet (P > 0.4; Fig. 5). However, fatter OVX females (21.5 ± 6.7% body fat, mean ± SD) tended (P < 0.1) to oxidize less of the increased fat intake (3.9 g intake and 2.2 g oxidized) than leaner OVX females (6.0 ± 1.8% body fat; 3.7 g intake and 3.8 g oxidized). Moreover, the change in fat oxidation with fat intakes across all three diets tended (P < 0.1) to be lower in the fatter females compared with the leaner females (0.7 ± 0.2 and 1.0 ± 0.01 g fat oxidized/g fat intake, respectively). There was no affect of body fat on fat oxidation in VAS male cats. Despite consuming 10 g less protein
on the high-fat diet, the fatter male and female cats increased protein oxidation, whereas the leaner cats decreased protein oxidation (P < 0.05). Body fat did not significantly influence carbohydrate oxidation (Fig. 5).

**DISCUSSION**

Short-term energy balance was not influenced by dietary fat content. The TEE measured in the cats in the present study was within the range previously reported for inactive cats (39–60 kcal/kg body wt; see Ref. 25). It was not surprising that TEE was equal to energy intake on both the low- and high-fat meat-based diets because the lower- and higher-fat diets were fed isocalorically at MER. Whether free access to the experimental diets would have affected energy intake, TEE, and subsequent weight maintenance is not known. The animals selected for this study previously maintained their weight (±5%) while consuming an ad libitum meat-based diet that varied little in fat content and that was similar in composition to the basal diet. Cats are able to maintain body weight when allowed ad libitum access to palatable, high-fat (>50% as energy) diets (8), and others have shown that cats have the ability to adjust intake according to energy density of the diet (20). Therefore, the current results are likely representative of most cats being fed meat-based canned diets. In contrast to cats, ad libitum intake of high-fat diets has been associated with hyperphagic effects resulting in weight gain in humans (12) and other animals (45, 46).

In the present study, TEE was not influenced by macronutrient composition despite large differences in protein content, 45 vs. 26% of energy in lower- and higher-fat diets, respectively. The large specific dynamic action associated with protein (~20% of protein energy consumed) suggests that the thermic effect of feeding would likely be increased on the low-fat diet. Individual components of energy expenditure were not measured, and any difference in the thermic effect of feeding due to diet was not reflected in TEE. Furthermore, 24-h protein oxidation, based on urinary nitrogen, did not match protein consumption. Despite consuming 10 g less protein on the higher-fat diet, the leaner cats only marginally decreased protein oxidation, whereas the fatter cats actually increased protein oxidation (Fig. 5). The lack of matching protein oxidation with protein intake in cats fed the lower- and higher-fat diets may be attributable to the inability of cats, unlike other animals, to increase protein oxidative enzymes with increasing dietary protein (6, 34). Cats have a high nitrogen requirement (17) and may conserve nitrogen to respond to fluctuations in dietary protein intake (32). The reason the fatter cat’s increased protein oxidation compared with leaner cats, despite consuming a lower protein diet, may be linked to an inability of insulin to inhibit protein oxidation as observed in obese humans (29). The increase in protein oxidation observed in the fatter cats when fed diets low in protein may portend a metabolic problem with amino acid metabolism that may be linked to hepatic lipidosis that occurs in obese cats who are anorexic (7).

Fat oxidation increased commensurate with fat intake. The current study provides evidence that sedentary cats, including OVX females, adapt to high-fat
meat-based diets by increasing fat oxidation as the fat content of the diet increased stepwise from 53 to 71\% of energy. The magnitude of the increase in fat oxidation was commensurate with the increased fat intake, sensitive to small changes in dietary fat, and was linear with a mean slope of 0.91 g fat oxidized/g fat intake. It has been proposed that the partitioning of macronutrients for oxidation is flexible, allowing for adjustment of macronutrient oxidation to equal the macronutrient composition of the diet (5). The decreased 24-h N\textsubscript{R}Q and consequently the higher fat-to-carbohydrate oxidation ratio that occurred with consumption of diets with increasing levels of dietary fat demonstrate that the cat possesses this metabolic flexibility. The metabolic flexibility of cats to match fat oxidation with fat intake may be due to feeding the cats at their MER or feeding a meat-based diet with little or no carbohydrate. The enhanced fat oxidation in the cat fed high-fat diets could also reflect unique metabolic characteristics of the cat.

Studies suggest that, when humans are in energy balance, the magnitude of change in fat oxidation is similar to the change in fat intake (19, 24, 26, 30). However, fat oxidation apparently does not keep pace with dietary fat intake under isocaloric feeding conditions in some humans, particularly obese and postobese individuals (5, 22). Indeed, Thomas et al. (43) demonstrated that obese subjects (>35\% body fat) did not increase fat oxidation after 7 days of consuming an ad libitum fat diet. In addition, individuals with low fat oxidation rates experience weight gain on weight maintenance diets (22, 47). The fatter female, but not male, cats tended (P < 0.1) to less precisely match fat oxidation to fat intake when challenged with a higher-fat diet than were leaner cats. The physiological significance of these results is not clear, but they might be relevant to the tendency of OVX cats to become fatter (16, 37). However, fat oxidation was perfectly matched with fat intake in the two leaner cats that were also ovariectomized.

There was no significant difference in fat oxidation between VAS male and OVX female cats either as total fat oxidation (P < 0.10) or fat oxidized per kilogram body weight (P > 0.6). However, when challenged with the higher-fat diet, VAS male cats increased total fat oxidation and fat oxidized per kilogram body weight more than OVX female cats (P < 0.001). The difference in fat oxidation in response to high-fat feeding between VAS and OVX cats could be due to the presence of testosterone in VAS male cats or the absence of estrogen in the OVX cats. Low doses of testosterone in puberty-delayed males promote fat oxidation (4), and the administration of estrogen to ovariectomized rats elevates fat oxidation in response to physiological stimulus (18).

Humans with histories of weight maintenance maintain fat balance on a diet relatively high in carbohydrate, whereas the cats in the present study maintained fat balance on a diet containing essentially no carbohydrate. Cats fed little or no carbohydrate have high rates of gluconeogenesis (21). It is therefore reasonable to assume that the carbohydrate oxidation measured in the current study, which greatly exceeded the carbohydrate intake, probably is derived from glucose produced from glycogen, lactate, and gluconeogenic amino acids via gluconeogenesis. The lack of carbohydrate in the carnivore diet probably facilitated the high levels of fat oxidation. Carbohydrate oxidation has been shown to occur at the expense of, or inhibits, fat oxidation (2, 10). The current results demonstrate that fatty acid oxidation is unimpaired in cats fed diets free of carbohydrate.

Other animals, unlike humans and the cats in this study, consistently gain weight when fed high-fat diets at MER (19, 33, 40). For example, dogs fed a high-fat diet gained excessive weight and increased body fat compared with dogs fed a low-fat diet (36). The authors speculated that small differences in energy intake (23 kcal/day) accounted for the excess weight gain. The increase in weight and body fat in animals fed high-fat diets at a constant energy intake is probably due to their inability to increase fat oxidation. Weber et al. (44) suggested that dogs have a limited ability to oxidize plasma free fatty acids. Flatt (13) also found that fat oxidation was negatively correlated with fat intake in ad libitum-fed mice.

Most cats maintain their body weight while consuming typical meat-based carnivore diets devoid of carbohydrate but rich in protein and fat. The current study provides evidence that sedentary cats who have previously maintained body weight while consuming ad libitum a variety of meat-based diets with a constant fat content can adapt to a higher-fat meat-based diet by dramatically increasing fat oxidation. Together with the lack of a hyperphagic effect of dietary fat per se (8, 20), the flexible response in fat oxidation on high-fat diets may account for the ability of the great majority of cats to maintain weight on what is a very high-fat diet for most species. Whether dietary fat plays a role in the development of feline obesity is not known; however, physical inactivity and neutering have been implicated as potential risk factors (16, 37, 39, 42). The current study found no evidence that inactive or gonadectomized female cats are unable to achieve fat or energy balance with short-term challenge of a high-fat meat-based diet. We speculate that the consumption of dry food containing significant amounts of added carbohydrate would seriously impair the cat’s ability to oxidize fat and possibly maintain weight under ad libitum feeding. Notably, more obese cats consume dry food containing carbohydrate than a meat-based canned diet (11). Further studies are required to determine whether these results may be extrapolated to felines in general, particularly those that are gonadectomized and those fed commercial diets containing significant amounts of carbohydrate.

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